ON THE THEORY OF NERVE-ACTIVITY.[1]

"A THEORY of nerve-energy would have to show how precisely those properties which are characteristic of the activity of the nerves result with necessity from the multifarious aggregate of the conditions constituting them."

I have taken these words from the *Manual of Physiology* of Carl Ludwig,[2] that memorable man, who achieved so much for physiology during his long connexion with the university of Leipsic. And now that I am about to develop a special view of my own relating to nerve-activity, it is both appropriate and requisite that I should apply the criterion involved in Carl Ludwig's words to the theory which I am to advance.

If I were asked whether this view could be considered as a contribution to the theory of nerve-activity in the sense indicated by that great master of experimental physiology, I should have to confess that such is not the case; for neither from their constitu tion nor from their form can I deduce with necessity that property which I am going to attribute to the nerves, however much I may be inclined to assent to Ludwig's dictum "that a nerve is indebted for its energy to its constitution and structure," and to a change in those for a change in its energy.

The source from which I have derived my views relative to the mode of activity of the nerve-fibers, lies quite remote from all the knowledge we now have of their structure and of their chemical and

[1]Academic Discourse delivered before the University of Leipsic, May 21, 1898. The German original has just recently been published by Veit & Co. of Leipsic.

[2]Second Edition, page 141.

physical properties, and I am therefore perfectly willing that the view which I have put forward as a contribution to the theory of nerve-activity should be regarded only as a conjecture concerning the same.

In justification of my position, however, I may add that even at best we are in possession only of conjectures concerning the real inner nature of nerve-activity. We know, thanks to Helmholtz, that any sudden alteration in the condition of the nerve-fiber caused by some stimulus, is propagated along the fiber with a measurable speed, and further, how great this speed approximately is. But the exact nature of that alteration, and the exact character of the process propagated along the fiber, we do not know. Dubois Reymond's classical investigations have made us acquainted with the electro-motor property of the nerve in its various conditions. But as little as a galvanic current gives us an explanation of the peculiarities of the chemical process to which it owes its origin, so little does the current derived from a nerve give us information concerning the peculiarities of the chemical change in the nervous substance. The assumption that chemical phenomena are the gist of the process which we are wont to designate as the activity of the nerve, is, of course, more than a mere conjecture. But in making such a conjecture we assert concerning the nerve nothing more than what might just as well be asserted of all living substances. And nothing is said which would characteristically distinguish the life of the nerve from the life of any other organ.

In fact, life is still as much of an unsolved riddle as it was when the so-called mechanical conception of vital phenomena overthrew the vitalistic, and awakened by its brilliant achievements the most sanguine expectations, foreshadowing results far beyond what has even yet been fulfilled, valuable and fruitful as this has been.

To whatever point the physical or chemical investigation of the animal organism has penetrated, it has always, sooner or later, come upon the mysterious action of the living substance of those elementary organisms of which the animal and the human body are composed. We have now learned modesty, and from having once believed that we had entered the holy of holies, we now acknowl-

edge that we have as yet scarcely passed the portico of the temple. Can it surprise us then that to-day the old fallacious doctrine of vital force which we imagined had been definitively vanquished, should again rear its head under new names? Let us confess that we ourselves are to blame for this because in the first exultation of success we promised more than we were able to fulfil.

Let us cease considering physiology merely as a sort of applied physics and chemistry and thus avoid arousing the justifiable opposition of those who believe it to be an idle task to seek an exhaustive explanation of the living from the dead. Life can be *fully* understood only from life, and a Physics and a Chemistry which have sprung solely from the domain of inanimate nature, and which therefore apply solely to inanimate nature, are adequate only to the explanation of such things as are common to the living and the dead.

This is very much, but it is not all, and I am fain to paraphrase here the words of a brilliant physicist[1] who has used them in an analogous connexion, and say: If the assertion that physiology is only applied physics and chemistry be taken to mean that the laws discovered in the domain of physics and chemistry are sufficient without extension and generalisation to explain fully the phenomena of life, "we are, in my opinion, confronted with a view which is in every respect comparable to that of Thales, who endeavored to explain everything from the properties of water. Think of the improbability of a wide domain of experience being absolutely exhausted by a narrower previously known one." If everything that took place in nature could be designated outright physical or chemical, whether it was subsumable under the present known laws of physics or chemistry or not, then naturally all phenomena of life would in such a case fall within the domain of physics and chemistry. But we cannot hoist our flag over a territory where we have never as yet set foot, much less explored.

At bottom, it was not the mere negation of vital force at this juncture that secured for physiology its brilliant successes, but rather, the concomitant introduction into biology of the rigorous

[1] E. Mach, *Die Principien der Wärmelehre*, p. 351.

methods of physical science and of the great mass of apparatus and appliances which had been created by those methods; and only in so far as vitalism persisted in employing unproductive methods for treating biological problems did it do real harm and was its overthrow of real benefit. In fact, every observed attribute of life which was susceptible of immediate physical explanation had already been physically explained in the heydey of vitalism. The laws of the lever had been applied to the movement of the human members, and the movement of the blood had been attributed to the contraction of the muscles of the heart, even at a time when the muscular activity itself was still conceived in characteristically vitalistic fashion. Even to-day we cannot explain this last-named activity, although it is one of the most palpable and most obtrusive of the actions of living things.

The impulse to resort to analogy and to carry over propositions abstracted from one domain into others is so great that there can be no fear that any phenomenon of life will long remain exempt from physical or chemical explanation after physics and chemistry have supplied the requisite means. To-day, the danger of precipitate and therefore of insufficient physico-chemical explanation of vital phenomena is perhaps greater than the danger that vital force should continue to be employed (to use a celebrated saying) "as the comfortable couch where reason is quieted upon the pillow of obscure qualities."

Even the mechanical theory of life has not been able to prevent the substitution of a new dogmatism for the old vitalistic creed, and in adducing a striking instance of this fact I reach the real subject of my present discussion.

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I have already stated that the process which is propagated along a nerve-fiber in the shape of a so-called excitation is in its real nature unknown to us. Nevertheless, it is accepted as an established fact by most physiologists to-day that this excitation is always of exactly the same kind, not only in one and the same nerve-fiber but in all nerve-fibers; and that it can consequently undergo alteration only with regard to the strength and time of its

propagation, but not as regards its quality; and that, therefore, all functional differentiation of the nerves is exclusively resident in either their central or their peripheral terminal apparatus. So thoroughly convinced are many physiologists of the truth of this view, that they absolutely refuse to consider any theory which assumes a qualitative variability in the excitations which pass through the nerve-fibers. And they do this in the consciousness that they are supported by the authority of a Helmholtz, a Dubois Reymond, and a Donders.

But let us examine for a moment the meaning of the assertion that the excitations are absolutely alike in all nerve-fibers.

If it were possible to insert a portion of a sensory nerve into the path of a motor nerve, and to connect the former with the latter, fiber for fiber, a cerebral excitation of the motor nerve would pass unaltered through the inserted piece of sensory nerve to the muscle, which it would forthwith set into activity. Or, if we could cut out a piece of the optic nerve and insert in its place a piece of a motor nerve, and combine every fiber of the former with every fiber of the latter, functional continuity would be restored along with the anatomical continuity, and the perception of light and color would be possible, just as before.

Finally, let us imagine the optic nerve and the auditory nerve severed, and each brought into conjunction with the other crosswise. According to Dubois Reymond, we should in such a case hear the lightning with the eye as a noise, and see the thunder with the ear as a succession of light-impressions.

Of such a character are the consequences that flow from the assumption that the functions of the nerve-fibers are all absolutely alike. The impossibility of actually realising the hypothetical cases which have been adduced affect in no wise the correctness of the conclusions drawn from them.

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What, now, are the considerations that could have lead to the enunciation of so definite an opinion regarding processes which are still involved in so much mystery for us? Carl Ludwig himself once considered the question of the likeness or unlikeness of the

nerve-fibers, and did so with all his wonted caution, but he finally left the question undecided, as did also Johannes Müller in his time. Since then, no new facts have been brought to light which could have tended to confirm the theory of the homogeneity of the nerve-fibers, as Ludwig called it. For the experiments on the grafting of the peripheral terminals of severed nerves, with the central terminal of a nerve having different functions, even if they had been successful, could not have decided our question. And yet, by the majority of physiologists the theory of homogeneity is regarded to-day as an established truth.

By his *Investigations in Animal Electricity* Dubois Reymond[1] believed he had "awakened into lifelike reality the hundred years' dream of the physicists and physiologists regarding the identity of nervous energy and electricity, even though in a slightly changed form." The facts which he adduced have been confirmed in all their essential points, and although their interpretation has turned out to be different from what he conjectured, yet the opinion which he cherished, according to which the essential nature of nervous activity found its expression in electrical phenomena, is still shared by many physiologists to-day. Now this view was in its time, and to-day is, so far as I can see, the principal foundation of the conviction which so generally obtains in the scientific world regarding the homogeneity of the nerve-fibers and of their excitations.

When we set a nerve in excitation at any point of its course by an artificial stimulus, the propagation of the process of excitation can be followed step by step along the path of the nerve by means of a galvanometer, for the reason that the electric behavior of the nervous substance changes precisely as the condition of the nervous substance itself changes in passing to the excited state. The galvanometer then shows us the current of action, or at the severed terminus of the nerve the so-called oscillation of the current of injury. It was rendered highly probable by Dubois Reymond (and later investigations have only confirmed the conjecture,) that these electrical phenomena are characteristic of all nerves, and that

[1] Preface, p. 15.

they accompany not only the excitations which have been produced by artificial stimuli, but also such as are disengaged in the natural way from the central or peripheral terminal apparatus of the nerve-fiber. If now the electric phenomena were the expression of the real inner character of the excitation passing along the nerve, the homogeneity of the latter would follow immediately from the homogeneity of the former; and different nerve-fibers could exhibit different behaviors only with regard to the intensity and time of action of the excitation.

It was afterwards discovered that the electric phenomenon in question admitted of scarcely any other explanation than that of a chemical process propagated along the excited nerve. Yet even this discovery could not shake the theory of homogeneity.

After that theory had once taken root, the identity of the chemical process was deduced immediately from the identity of the electrical behavior, and the idea never suggested itself that we might with just as good reason infer the identity of two chemical processes from the identity of their thermal effects, or the identity of the chemical transformation in two galvanic elements from the identity of their currents.

The electrical phenomena which accompany the excitation of the nerve furnishing no adequate foundation for the theory of homogeneity, the next natural support likely to be resorted to for this theory is that of the morphological and chemical homogeneity of the nerve-fibers. It is quite true, we are as yet unable to distinguish by the microscope and by chemical reactions every motor fiber from every secretory fiber, and every optic fiber from every auditory fiber. But the cases are numberless in which living elementary structures having different functions exhibit absolutely the same behavior when subjected to known optical or chemical tests.

The germs of quite different species of animals are frequently so much alike as to be confounded with one another; and the germs of different individuals of the same species naturally show a still greater degree of similarity. Yet no biologist has the least hesitation in ascribing to each individual germ some quite specific individuality, some personal idiosyncrasy, so to speak, of inward struc-

ture or molecular constitution by virtue of which a perfectly definite path of future development is marked out for it.

It is regarded as almost certain that the different functions of the secretory cells of the various glands are attributable to the physical and chemical differences of their vital substance, and yet in many cases it would be quite impossible by the microscope and micro-chemical methods at our command, to determine the actual function of any single glandular cell.

It was shown by Max Schultze many years ago, and recent inquiries have confirmed his results,[1] that while the pseudopodia of the same rhizopod merged and fused perfectly on contact, the pseudopodia of different individuals of the same species would not fuse on being brought together. Now, if the protoplasm of two individuals of the same species were absolutely of the same composition, it would be difficult to see why their pseudopodia should not behave with regard to one another precisely as the pseudopodia of the same individual do.

We are obliged, accordingly, to attribute to the living substance of every single one of these minute and inferior creatures, specific individual properties, by virtue of which their substance is distinguished from the substance of every other individual of the same species; although there cannot be, even in so patent a case as the present, the remotest thought of directly demonstrating these inferred differences by the experimental means of investigation at our command.

But if a distinctive individual stamp must be imputed to every one of the countless members of the same rhizopod species, why shall some such distinctive mark be refused to the elementary organisms of which the nervous system is composed? The fact that the rhizopods lead an independent life, while the nerve-elements are rigorously subordinated parts of a more highly developed organism, is no reason whatever for our not doing so, seeing that each individual nerve-fibre is connected with a vast and most varied host of

[1] Paul Jensen, "Ueber individuelle physiologische Unterschiede zwischen Zellen der gleichen Art." *Pflüger's Archiv für die ges. Physiologie.* Bd. LXII., p. 172. 1895.

vital functions, and that consequently it can according to the principle of the division of labor be highly differentiated; whereas no such division of labor can come into consideration in the case of the individuals of a rhizopod species.

In this division of labor of our organism lies, in fact, part of the answer which I should give to the advocates of the theory of homogeneity, if they were to ask why I am anxious to assume heterogeneity in places where the assumption of homogeneity appears to be adequate to explain the function of the nerve-fibers as simple organs of conductivity. The argument that I have adduced, they would contend, proved at most that the sameness of all the fibers cannot now be directly demonstrated, that there are even reasons for suspecting them to be not the same, but that in any event no counterproof to their theory is furnished. Even the wires which conduct electricity, they would say further, may be put to very different uses, and yet the electrical phenomenon in the conducting wires is qualitatively the same. The fact that the excitation of a glandular nerve produces a secretion, while that of a muscle-nerve produces a movement, is sufficiently explained by a difference in the terminal apparatus upon which those nerves act; and just so much ground and no more is there for supposing a qualitative difference of excitation to result from a difference in the stimuli by which the nerves of the several sense-organs are excited. The further fact, they would continue, that sound is able to excite the auditory nerve and light the optic nerve is due entirely to the different structure of the apparatus at the peripheral end of these nerves,—one apparatus being especially adapted for the reception of sound-waves and the other for the reception of light-waves and for their transformation into nervous excitation. If the sound were to strike directly upon the auditory nerve itself, and not on the peripheral apparatus, if the light were to fall directly upon the optic nerve itself, these nerves would not be excited,—a proof that the so-called specific excitability of the various sensory nerves is not due to any dissimilarity of the latter, but entirely to the differences of the terminal apparatus which receive the impression.

In answer to this oft-repeated argument, it must be frankly

confessed that so far as our present knowledge goes, no conclusion whatever follows from the varying behavior of the sense-organs toward different sensory stimuli in favor of the assumption of a specific heterogeneity of the sensory nerve-fibers; but neither does anything follow in contravention of such an assumption. And it must be further admitted that considering the dissimilarity in results which follow upon the excitation of nerves that act centrifugally according as they set a muscle or a gland in activity, no conclusive argument is forthcoming either in favor of or in contravention of the homogeneity of these nerves.

But the situation assumes a different aspect when we consider the manifold results to which the excitation of such sensory nerves leads as have not their terminus in such heterogeneous organs as the muscles or the glands, but all end in the brain. For instance, we are compelled to inquire how it is that the excitation of one nerve brings with it the sensation of light and color, that of another the sensation of sweet and sour, that of a third the sensation of heat and cold, while at the same time all these nerves carry to the brain excitations which are absolutely the same in quality. To this the theory of homogeneity has always answered without the least ado that it is because the like nerve-fibers of the tongue and of the eye lead to unlike nerve-cells in the brain, some of them to cells whose specific character enables them to take up the excitatory conditions that correspond to the sensations of taste, others to cells which conformably to their specific function respond to the excitation of the fiber with precisely that physiological process whose psychical correlate is a sensation of light.

And here finally we are met with the frank concession that that interior commotion of the nervous substance which we call excitation or activity is, at least in the various sensory centers of the brain, specifically differentiated, and that here at last the functional homogeneity reaches its termination.

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While this doctrine was taking its development,—a doctrine according to which all the nerve-fibers are exactly the same in kind, but the terminal apparatus which are functionally connected with

them are different in kind,—the idea necessarily suggested itself of separating the nerve-fibers as a particular group of elementary structures from the nerve-cells; but, even at the period of the development in question, it would have been quite admissible, in view of the anatomical continuity which had been established in numerous instances between cells and fibers, to have inquired by what right physiologists ascribed to the cells functions which varied in character, whereas they denied to the fibers connecting them all specific dissimilarity whatever, and that they did so in spite of the fact that chemical and physical research had not been able to discern any more characteristic differences in the substance of the cells than it had in the axial cylinder of the fibers.

Since that time, a different conception of the elementary structures of the nervous system has found almost universal acceptance. Every nerve-fiber, according to this theory, is associated in such wise with a nerve-cell as to form with it a single elementary organism only; and the living substance of that organism, which is collected in more abundant quantities about the nucleus of the nerve-cell, is continued into the fibers. Accordingly, the nerve-fibers would be integral constituents of these elementary structures of the nervous system, or *neurons*, as they are called. On this theory, the idea is quite natural to ascribe to the fibers which continue the cells the same specific differences which physiologists were obliged to assign to the nerve-cells of the various cerebral centers.[1] But as soon as we do this, we no longer have before us cells which, though capable of performing different tasks, are yet connected by filaments having quite the same functions, but we have elementary organisms whose specific or individual dissimilarity extends to their remotest filar prolongations. A nerve-trunk is no longer a mere bundle of conducting wires disengaging different sorts of effects according to the kind of apparatus with which they are connected at their termini and being at the same time in their own specific function absolutely of the same kind; but it is a bundle of living

[1] I offer no opinion as to the correctness of the histological doctrine of neurons. I lay it at the foundation of the present discussion because my theory needs some definite histological substratum.

arms which the elementary organisms of the nervous system send forth for the purpose of entering into functional connexion with one another, or of permitting the phenomena of the outside world to act upon them, or of exercising control over other organs like the muscles and the glands. And in each one of these arms a quite special kind of life is active, corresponding precisely to the neuron to which the nerve-fiber belongs. The conducting path which unites a sense-organ with the cerebral cortex, or the latter with a muscle, appears as a chain of living individuals of which every member, although always dependent upon its neighbors, still leads a separate life, the specific character of which is generally different in the different parts of the nervous system. Even in the neurons of the same group it is not absolutely the same, but bears in each of them a more or less individual stamp.

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The theory of the homogeneity of the excitatory process in all the nerve-fibers involves the further assertion that this process remains qualitatively the same in one and the same fiber, and that it is variable only as to intensity and time of propagation.

I once advanced views relating to the processes in the nerve-apparatus of the visual organs which presupposed that in one and the same retinal element different processes could be set up by light-waves of different rates of vibration. The physiologists declared such a view inadmissible inasmuch as more than one process in the same structural element would presuppose more than one conduction-process in the corresponding fiber, a view which physiology was forthwith compelled to repudiate.[1] And this dogma, according to which every nerve-fiber is held to be capable of only one kind of excitation, had actually been extended also to the nerve-cells. True, as already said, physiologists were even then compelled to ascribe to the nerve-cells of the different sensory centers different functions ; but in one and the same cell the excitation was said to be of unalterable quality.

It was no less an authority than Helmholtz who introduced this

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[1] Donders, "Ueber Farbensysteme," *Arch. f. Ophthalmol.*, XXVII. 1881.

conception into the physiology of sensation, and to-day his disciples still esteem the doctrine of cerebral cells sensitive only to red, green, or violet, as the rarest fruit of Johannes Müller's doctrine of the specific energies of the sensory nerves. But I am convinced that Johannes Müller would not have accepted such a view, for his conception of biology was thoroughly monistic, and he would not have denied to the cell of the brain what must be conceded to the lowest unicellular organism, namely a more or less wide qualitative variability of its inner life.

Who can deny that the chemical changes in the substance of an infusorian vary qualitatively according to the changes in its external life-conditions; for example, in food material, or in other stimuli acting upon its body? And even granting that the progressive division of labor which accompanies the increasing structural complexity of the animal organism, in general brings more structural uniformity into the life of the individual cells, still there is no ground for the view that just in the nerve-cell this uniformity can become as complete as the homogeneity theory demands.

Granting, however, the possibility of qualitatively different excitation-conditions in the same cell (and in the fiber springing from it), then there is opened for the theory of nerve-life a series of points of view which are quite excluded by the homogeneity theory.

At the outset it follows that a neuron which is capable of various kinds of activities, will possess a correspondingly complex excitability, that is to say, it will vary in its reactions according to the nature of the stimuli, it will respond by one or another of its habitual special activities; in brief, the activity of the neuron and of its fiber may vary, not merely, as has been supposed, in intensity but also in quality, according to the nature of the stimulus, whether this be exercised by an external sense-organ, or by an adjacent neuron. A further consequence of our view would be that the effects in those non-nervous elementary organs with which centrifugal fibers stand in functional connexion, might also vary with the kind of excitation conducted in the fiber.

For the motor fibers, of course, there is, owing to the uniform

action of the muscle-fiber, no apparent reason for such a view. It is otherwise, however, with the nerve-fibers which govern the activity of a gland. The view now generally accepted is that, in conformity with their unalterable homogeneity of excitation, these secretory fibers can influence the activity of their dependent gland-cells only quantitatively. But how would it be if, according to the nature of the excitation given by the nerve-fiber, the chemical processes in the secretory cells were different, and consequently the nervous system could affect, within certain definite limits, the *quality* of the secretion furnished by one and the same cell?

And would not similar views hold in regard to the so-called trophic activities of centrifugal nerves? Inasmuch as these activities do not, as in the case of the motor or secretory nerves, immediately reveal themselves by easily demonstrable movements, they have hitherto remained rather within the domain of conjecture than in that of safely ascertained facts. If, however, the nervous system exerted an immediate influence, not merely on the motor and secretory, but also on the other elementary organs of the body (e. g., on certain epithelia, on the developing cells of the ovary, etc.), then here too the answer to the question whether such an influence were variable only according to quantity or also according to quality, would be of far-reaching influence.

But let us turn back to the activities which the excitation of a neuron exercises on those other neurons with which it is connected.

If, as histology teaches us, a sensory fiber entering the spinal cord divides into an ascending branch and a descending branch, and from these latter there branch off the so-called collaterals which finally stand in relation with other neurons (it matters not whether through direct contact or through connection); if finally every one of these neurons by its branching stands in functional relation with still others, and so on; then, from a purely anatomical standpoint, there exists for an incoming excitation an incalculable multiplicity of paths through the central nervous system. If now an excitation which has seized a neuron, should pass on indifferently to all the other neurons with which the first is functionally connected, there

would result an exceedingly wide-spread diffusion of the excitation entering through a sensory fiber or coming from a neuron to the cerebral cortex, a diffusion such as is not known to exist, or, at the most, is only approximated to in motor effects under pathological conditions.

It must consequently be assumed that the excitation of a fiber does not take indifferently all the anatomically given ways, but selects predominantly certain determined paths, diffusing itself in the others only in a more or less enfeebled manner or only exceptionally; and the question hence arises: What is the determining factor for this choice, and for the varied ratio of the strengths with which the excitation propagates itself along the many possible paths?

The homogeneity theory finds the answer in the different degree of excitability and conductivity of the individual paths, and in the different amounts of resistance offered to passage from one neuron to another. As for the further diffusion this is made to depend entirely on the strength of the incoming stimulus.

Numerous facts from the sensory and motor territories of nerve-life teach us that the innervation issuing from a neuron can diffuse itself in the nervous system very differently according as certain other excitations take place at the same time. For example, though the stimulus be the same, a reflex movement is sometimes reinforced and sometimes inhibited by excitations issuing simultaneously from another place on the periphery of the body or from the brain. Accordingly, the homogeneity theory accepts the view that resistance to conduction in a neuron can sometimes be increased and sometimes lessened by excitations which reach the same neuron from another direction, in other words that sometimes a so-called path-breaking, sometimes an arrestation takes place; but it does not further explain how excitations which are said to be always of the same kind and to differ only quantitatively, can at one time operate on the neuron so as to promote, and at another time so as to arrest, its function.

Everything is seen in a different light, however, as soon as a qualitative variability of the conducted excitation, and also a quali-

tatively different excitability of the conducting paths, are admitted. If the individual nerve-fiber is suited for the taking up and transmission of definite qualities of excitation, either preferentially or exclusively, *then the path which is taken by an excitation is coincidently determined by the quality of that excitation.*

As a report is principally taken up and circulated by those who take a special interest in it, that is to say, the paths of its spreading depend on the nature of its contents, so to a definite afferent excitation those neurons will react preponderatingly whose peculiar nature precisely corresponds to that excitation.

The mutual relations of neurons will then depend not merely upon their anatomical arrangement, but also on their degree of internal structural affinity. And as one and the same fiber need not be adapted merely to *one* kind of excitation, but may be adapted to a certain number (though within a narrow range), so not only will the same path be able to conduct various kindred qualities, but the excitation issuing from the same neuron will be able, according to its particular quality, to penetrate various parts of the nervous system.

If, further, excitations should be simultaneously brought to the same neuron by two of its neighbors, then according to the homogeneity theory these excitations could on meeting only strengthen or weaken each other. According to our view, however, the two excitations could be of different kinds, and from their meeting in the same substance might originate a new quality, which would indeed be closely related to the two single excitations, but not like either.

And generally the whole life and being of the nervous system, its ontogenesis and phylogenesis, appear in a totally different light as soon as we give up the dogma of the absolutely homogeneous function of all nerve-fibers, and ascribe to the individual fiber-groups and fibers specifically or individually different biologic characters. For that dogma excludes from the neuron every capability for development and improvement, in so far as such capability is not already inborn and in so far as it is not a mere augmentation

of its excitational or vital process, which latter is from the beginning to the end of its life supposed to be peculiar and unalterable.

Rightly have the opponents of the doctrine of the specific energies of the sensory nerves pronounced against the view of a life-long unalterable constancy of function of the nerves, but they went, as I conceive, too far when they contested the congenitally different and special nature of the individual sensory nerves, accepted the indifference of function of all sensory fibers of the new-born, and regarded all functional differences of nerve-fibers, which are the phylogenetic acquisition of innumerable generations, merely as the result of an adaptation to heterogeneous, individual sensory stimuli during the post-embryonic period.

Of course after birth the influences of the external world belong to the conditions of the further normal development of the whole body, and the sensory stimuli especially are indispensable conditions of development of the nervous apparatus of our sense-organs. But light, for example, finds in the eye of the new-born babe not a nerve-substance from which, so to speak, anything whatever can be made; in other words, a substance which, if it could be transposed from the eye into the ear or into the tongue could be educated by the sound-waves to be a medium of auditory sensations, or by gustatory stimuli to be a medium of taste-sensation.

As the germ sprouting from the earth needs light to become a green plant, so in the new-born babe the neuron in the eye needs light, and the neuron in the ear the sound stimulus, to complete its course of development; but just as light never makes the fungus green, so it could never make the neurons of the ear see if they should be transplanted into the eye. As I take it, the neurons of our eye are not merely *educated*, but are *born* for seeing, and likewise those of our ear for hearing.

This, however, does not exclude the fact that, within their own narrow congenital limits of existence and action, they are capable of further individual development. And the same holds good (sometimes more, sometimes less so) of all parts of our nervous system. It is true, the farther back in the immeasurably long developmental series of the animal organism a given part of it can

be traced, the more fast and sharp is the congenital stamp of its function, and the less capable does it appear of transformation and development in the course of its further life. But the cerebral cortex is reckoned among the phylogenetically youngest parts of our nervous system, and its neurons belong, as it seems, to those elementary bodily organs which in post-natal life are afforded the relatively widest sphere of individual action under the influence of impinging stimuli. Now, how is such a development conceivable if the internal activity of a nerve-fiber, or a nerve-cell, in brief a neuron, is to be always of one and the same kind?

What is it then that a neuron of our cortex under normal circumstances experiences? In other words, of what do the stimuli which encounter the same and determine its internal activities, consist? Under constant conditions of nutrition, these are mainly the excitations conducted to it from those other neurons which stand in relation to it by means of the nerve-fibers. If, however, these nerve-fibers always conduct to it only the same kind of excitation, have, so to speak, only one note to their lyre, and therefore the stimuli which the neurons experience throughout life are the same and are variable only in quantity and time, then the reaction of the neuron will also always be one of the same kind, and the afferent stimulus can only liberate in the nerve-cell forever *the same* activity. And if, as the homogeneity theory concedes, the latter could be different in the different nerve-cells, still in one and the same cell, and in so far as it depends upon the afferent excitations, it would remain the same its whole life long.

It will be altogether different, however, if these excitations vary qualitatively, according to the nature of the neighboring neurons from which they come, or if the afferent excitation from one and the same neuron may vary within certain qualitative limits. Then a more or less rich multiplicity of excitations will take the place of the just-mentioned monotony that the neuron experiences from its neighbors, and, as this neuron is in its turn capable of heterogeneous activities, there is also opened to it the possibility of reacting to different impulses in different ways.

The nature of this reaction will, of course, also be determined

by the inborn individuality of the neuron; but of the entire stock of innate qualities which it brings with it from birth those will be most fully developed in the course of its life to whose development the neuron is most frequently or most strongly excited by its neighbors. Or, briefly stated, the neuron will possess the capability of qualitative and not merely of quantitative development, which last would, according to the homogeneity theory, alone be possible to it.

According to its place in the nervous system, its more or less manifold relations to other neurons and its inborn structure, this subsequent development will be more or less many-sided, and the doctrine of the homogeneity-theory that the sameness of excitation which the neurons experience conditions a corresponding uniformity in their further development, may perhaps approximately hold for entire large groups of neurons. On the other hand, however, all experience or training both sensory and motor,—in brief, everything that can be called conscious or unconscious memory in the widest sense of the word,—is to my mind not conceivable unless the living substance of the nerve-cells and fibers is capable of a qualitatively variable development.

I have sought in vain in the writings of those supporters of the homogeneity theory who have occupied themselves with considerations concerning the physiological foundations of nutrition and exercise, for a satisfactory conception of the subject. For an explanation of the development of the central nervous system corresponding to the psychical development, we are with reason directed to the possibility of the origin of new connections between the neurons, to alterations of excitability and conductivity in the paths already provided, to the opening and the increasing erosion of certain old paths by use, etc. On all these, old or new, pervious or impervious paths, however, that which is conducted through the nerve-fibers still remains (according to the homogeneity-theory) always the same, and everywhere it is a matter only of moreness or lessness and of variable velocity. The whole nervous system, according to this theory, appears like a land whose numerous communities are connected by a richly developed network of roads, on which latter,

however, always and everywhere, only one and the same kind of wares is transported.

Writers love to compare the nerve-fibers with telegraph or telephone wires, and they will consequently, perhaps, point to the endless multiplicity of things which can be transmitted through wires of exactly the same kind. The comparison is seductive, for if spun out farther, it seems suited to solve all difficulties at a single stroke.

In place of the undoubtedly "obscure" specific or individual "qualities" of the nervous processes of which I have spoken, appears a multiplicity of oscillations of different temporal and spatial form, of which the nerve-substance is the mere *vehicle*. But one finally comes to exactly the same result with this comparison as I do. For one must admit that neither in all nerve-fibers is the same oscillation-form always transmitted, nor is every individual nerve-fiber susceptible of all the oscillation-forms which are possible to the nerve-substance generally, but only of those to which it can respond.

What we have named the specific energy of the fibers or cells reappears here as special resonance-capacities corresponding to definite oscillation-forms. What we formerly called an inborn, acquired or individual characteristic, becomes here the pitch; and, as with us, the specific excitabilities, so here the resonance and previous attunement of the neurons determine the paths in the nervous system which a given oscillation-form shall enter upon.

We accordingly acquire only another mode of expression for one and the same thing; and, as I conceive, one not corresponding so well to the facts, inasmuch as it takes no account of that which in an entirely unique way characterises all life, namely metabolism, that chemical change in the living substance whose qualitative differences it is at present (and may be forever) impossible to express by purely quantitative spatial and temporal terms.

From all that has been said it immediately follows that I not only agree with the teaching of Johannes Müller, but would like to see the scope of his conception much broadened. The specific energies are, according to my view, a phylogenetically acquired

heirloom, not merely of the sensory nerves, but more or less of *all* neurons, of their fibers as well as of their cells. But I consider that the inheritance allotted to the individual neuron is by no means so sparing and uniform as was assumed in the case of the cells of the sensory centers, and further that it was not bequeathed with a codicil that the heir should not add any newly acquired riches to his nheritance.

E. HERING.

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